University of Nevada, Reno

Rehabilitation of an agricultural wetland: Utilizing seed bank data to inform restoration and management.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal and Rangeland Sciences

By

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ABSTRACT

Wet meadows are ecologically significant and economically important areas that occupy a relatively small percentage of the landscape. They are at especially high risk because management of these lands for agriculture often require hydrologic modifications and eradication of native dominant species. Studies suggest that after cultivation or grazing ceases, important structural components of vegetation that used to be dominant may not spontaneously re-emerge. Dominant species are important because they control ecological processes that determine wetland function. These statements suggest that once these species are no longer dominant, wetland function is compromised, and restoration of ecological function requires reestablishment of the prior plant community composition. In this study we asked whether formerly dominant species could establish following agricultural abandonment and explored relationships between the seed bank composition with depth to ground water data and biomass accumulation. We hypothesized that resistance to weed invasion is a function of the maintenance of community functional groups, meadow hydrology, and biomass management.

A seed bank study of Winters Ranch, Washoe County Nevada was conducted from October 2014 to October 2015. A greenhouse seedling bioassay identified total of 2,416 seedlings and 33 plant taxa were observed in the seed bank, of which eight were native perennial bunchgrasses, 15 native forbs, four exotic grasses, and six were exotic forb species. The average viable seedling densities ranged from 6.8 seedlings/m^2 to 147 seedlings/m^2. The most common seedlings in the bioassay included *Bromus tectorum* (cheatgrass), *Bromus arvense (*Field brome), and *Apera interrupta* (silky bent grass), which are exotic winter annual species. An important finding was that the seedbank was not necessarily indicative of the aboveground vegetation. Some sampling plots revealed a seedbank dominated by late seral species, such as *Deschampsia cespitosa* (tufted hairgrass), a native graminoid that historically dominated wet meadows but is now only a minor component if not completely missing from meadows suggesting that some areas have the seed bank potential to return to a late seral state. Other plots were dominated by exotic annuals which were significantly correlated with deeper litter (thatch). These plots were in areas with deeper depth to ground water during the drought suggesting that a lack of decomposition is due to lack of soil moisture. Seed bank studies may be more important than above-ground surveys to indicate which areas are most likely to have problems with invasive species.

Management Implications

Management of fallow fields, particularly those with altered hydrology (lack of irrigation, diversions, ground water pumping) and slower decomposition will likely result in unexpected weed infestations and require the most effort to restore.

Keywords: Agricultural wetlands, decomposition, thatch, litter, seedbank, ground water, *Juncus arcticus, Carex nebrascensis*, *Deschampsia cespitosa*, *Bromus tectorum*

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INTRODUCTION

The seedbank is the reserve of viable seeds in the soil. The longevity of a particular species in a community is partially dependent on the plants' ability to produce seeds that can remain viable in the seed bank until suitable germination conditions occur. Soil temperature, water content, and light are the main environmental factors driving seed germination and emergence (Forcella et al., 2000). Knowledge of the seed bank and germination requirements in relation to litter depth, ground water, and timing for each species' seed emergence is important for effective weed control or re-establishment of late seral species.

At the community level, the seed bank influences succession after disturbance (Pakeman and Small, 2005). Over the last decade researchers have been assessing seed density and species richness in a wide range of plant communities. These studies have led to the general hypothesis that the similarity between seed bank and vegetation is expected to decrease with increasing community stability and lack of disturbance (Bossuyt and Honnay, 2008; Thompson and Grime, 1979; and Chang et al., 2001). Dissimilarity between the seed bank and vegetation is generally a consequence of the seed bank containing a high abundance of r-selected, annual and biennial species while the standing vegetation is composed of k-selected, later successional, perennial species. Over time and in the absence of disturbance, the perennial late seral vegetation matures and the similarity between seed bank and vegetation decreases (Fenner, 1985). However, in agricultural wetlands subjected to flooding events, natural flood cycles (disturbances) may never allow the wetland to return to the late seral state because flood waters transport seeds from an unwanted source. In addition, management activities including cultivation and grazing may eliminate species that produce late seral seed further promoting establishment of undesirable weeds.

Succession and vegetation

Archer (1989) reported that a disturbance to a plant community may result in the establishment of a different community, thereby altering ecological processes including nutrient cycling and energy capture (photosynthesis). Studies conducted in Europe and north America suggest that, after cultivation or grazing ceases, important structural components of vegetation that used to be dominant may not spontaneously re-emerge. In addition, after disturbance, wetlands often are being colonized by monocultures that have adapted to reproduce vegetatively, and biodiversity decreases. For example, when agricultural wetlands are intensively grazed, certain species decrease under grazing pressure including the once formerly dominant species of many wet meadows in Nevada, Deschampsia cespitosa. This species is replaced by monocultures of unpalatable species such as Juncus arcticus (Hoag et al., 2012). Juncus produces large amounts of biomass and with its high lignin levels Juncus litter is difficult to decompose. Potentially, the site could cross an irreversible threshold that, in order to return to the pre-disturbance vegetation structure and associated ecological processes, may require significant intervention.

Litter and decomposition

Species composition and structure have an effect on ecological processes including decomposition and nutrient cycling. In turn, the lack of decomposition of standing dead from those species can have an effect on the feedback loop of regenerating organic material capable of retaining water.

Thatch or surface litter is comprised of a layer of dead and living stems and roots that develops between the soil surface and the leafy foliage canopy. Surface litter accumulation occurs when the production of the plant tissue exceeds decomposition. In addition, in a grazed system, species that exhibit anti-quality components are those that are selected against because they are indigestible or cause bloat and remain when grazing ceases. Compounds that retard decomposition include lignin and waxes and are the primary compounds found in thatch (Smiley 1981). Due to the high lignin content, members of *Juncaceae* (a species not preferred by livestock) have been shown to have some of the most slowly decomposing leaf material in freshwater ecosystems (Webster and Benfield, 1986; Kuehn and Suberkropp, 1998).

Depth to groundwater, decomposition, and seedling establishment

Not only is the rate of decomposition influenced by plant composition and volume, but also by microbial processes. These processes are dependent on environmental conditions including aeration, temperature, and moisture. Poor aeration through excess water is associated with thatch accumulation (Beard 1973) because plants are not able to access oxygen through their roots. Alternatively, when a wetland is dried from hydrologic alteration, the moisture necessary to feed microbes responsible for decomposition is reduced and decomposition is slowed depending on the prevailing moisture content.

Plant establishment can be limited by presence of a thatch layer. Plants suffocate due to reduced light underneath the thatch layer which can halt physiological growth (Goodson et al., 2001). For example, it has been found that the aggregate of thousands of arched culms of *Juncus* greatly reduces the amount of available light that penetrates the canopy, negatively affecting species richness and abundance (Ervin and Wetzel, 2002). As a result of decreased plant growth and a lack of species richness, plant basal coverage decreases and bare ground increases under the thatch layer. This surface structure can provide increased germination sites in a more humid microenvironment ideal for inbibition of seeds (Facelli et al., 1999).

Under ideal conditions, standing dead material on flooded sites have more rapid decay rates than plant growth (Brinson et. al., 1981, van der Valk et al., 1991, Merritt and Lawson, 1979) and moisture levels that favor rapid decomposition of surface litter can in turn create space for perennial grasses to expand which act as a mechanical barrier for emerging seedlings (Nilsson and Grelsson, 1990; Facelli et al., 1991).

In conclusion, the rapid rates in production and senescence of culms, coupled with slow decomposition rates from reduced soil moisture can result in excessive litter buildup, loss of desirable plants, and an increase in bare ground. Increased bare ground could facilitate invasion of exotic plants leading to a reduction in site resilience and a positive feedback mechanism favoring exotic plant dominance.

In the case of an abandoned agricultural field where late seral, palatable species may disappear entirely, invasive species can proliferate across the landscape and disturbed wetlands that were once resistant to invasion come under significant threat. Despite the above characteristics of species that remain following grazing and their widespread distribution, no studies exist that directly measure the effect of their aggressive growth habit and slow decomposition rate on the surrounding vascular plant community and seed bank in a drying wetland. The main premise of this study was to determine dominant species present within the seed bank of different plant communities (as presented by monocultures of field sedge, Nebraska sedge, Arctic Rush, and creeping wild rye) and to explore patterns between the seed bank composition with depth to ground water data and plant litter accumulation. Our overarching hypothesis is that resistance to weed invasion is a function of the maintenance of community functional groups, meadow hydrology, and plant litter management.

Research questions

1. **How does the seed bank vary among the different communities?**
2. **How does emergence/presence of plant species relate to litter and depth to ground water?**

For question two, I focused on the responses of cheatgrass (*Bromus tectorum*), perennial natives, historic species, wetland (FACW/OBL) species, and *Deschampsia cespitosa*.

METHODS

Project Site Description

The study site was located in the Washoe Valley, Nevada (39º18’49.84”N, 119º49’02.59”W) at approximately 1545 m in elevation . This area is contained within the “cold desert” region of Land Resource Region (LRR) D, north of the hot desert and east of the Sierra Nevada Mountain range. The site is a complex mosaic of wet and dry meadow ecosystems associated with Ophir, Browns and Winters creeks, interdigitating with the emergent marsh complexes of Scripps State Wildlife Area managed by the Nevada Department of Wildlife (NDOW) to the east. Over time, hydrology of the meadow system has been drastically altered by irrigation, de-watering, and the establishment of State Highway 395 that dissects the meadow north-south on the west side and the historic Virginia and Truckee railroad. The legacy irrigation ditch system functions today as a conveyance during periods of high water and a vector source for seeds (Appendix A).

Browns, Ophir, and Winters creeks, originate approximately four miles to the west of the ranch as high-elevation, spring-fed streams of the Carson Range in the Humboldt-Toiyable National Forest. After moving through high-gradient stream channels they are funneled through a series of culverts under State Highway 395 before reaching Winters Ranch where they meander through sections of the meadow before draining into Washoe Lake. Several of the vegetation communities are augmented and influenced by these ephemeral water sources, while other communities are affected by water backfill from Washoe Lake. Additional areas are influenced by the railroad grade and ditch system.

The upland area adjacent to the ranch consists of non-native/naturalized pasture and sagebrush communities. Ecological sites within the wetland complex include the Dry Floodplain R028AY025NV and Wet Meadow 14+" P.Z. R026XY054NV (U.S. Department of Agriculture. 2003). The average elevation is 1554 meters. Species associated with the driest portions of the meadow include basin big sagebrush (*Artemisia tridentata* var. *tridentata)*, and rubber rabbitbrush (*Ericameria nauseosa*), that are beginning to dominate (unpublished Stringham data 2012 Appendix B). Beardless wildrye (*Leymus triticoides*), saltgrass (*Distichlis spicata*), western wheatgrass (*Pascopyrum smithii*) and Arctic rush (*Juncus arcticus*) are common in the dry meadow. The wetter parts of the meadow that are more connected to the three creeks and/or shallow groundwater include Nebraska sedge, Arctic rush, creeping bentgrass (*Agrostis stolonifera*), and annual hairgrass (*Deschampsia danthonioides*). Small pockets of tall white-top (*Lepidium latifolium)* and Canada thistle (*Cirsium arvense*) are present throughout the property. *Deschampsia caespitosa,* which was possibly a dominant species prior to agriculture, is a minor component throughout wetland sites that are inundated during the growing season indicative of facultative wet indicator status (FACW) and obligate wetland indicator status (OBL) vegetation (Reed, 1988). A reduction in water and a lack of vegetation removal (either by fire or grazing) has created a system with significant thatch build-up, changing not only decomposition rates but species composition. Sections of the meadow are composed of large monocultures of relatively unpalatable field sedge and rush, with pockets of Canada thistle and tall white-top. Other areas are more diverse with Nebraska sedge and associated weed components, and shallow ephemeral pools with saline tolerant species of Nuttall's alkali grass and salt grass.

Average precipitation equals 196 mm most of which falls as light to heavy snow or light rain from early November to early March. This site is typically windy with the strongest wind occurring in late March with high winds averaging 47mph out of the west and southwest. The warm season typically lasts from mid-June to mid-September with an average temperature of 27ºC with highs over five years averaging 39ºC. The cold season from mid-November through mid-February averages 11ºC, the coldest temperatures in January average -18.8ºC (Western Regional Climate Center, Washoe Valley, NV).

The soils on the site are deep, poorly to moderately well-drained. Landslides from nearby Slide Mountain contribute to presence of a sandy to loamy course sand layer in the A horizon from 0 to 30. The soil beneath the surface horizon is a sandy loam soil and extends down to 80 cm. The pH ranges from 6.6 to 7.4 and redox features persist throughout the profile. Soils are classified mesic Fluvaquentic Endoaqualls (NRCS Soil Survey Staff, 2016).

Irrigation has been practiced in many wetlands throughout the arid West for more than 125 years, and this timeframe likely applies to the wetlands at Winters Ranch. Winters Ranch was used for pastures and cultivation but after 2002 (2005 in the southern end) the area was abandoned and left fallow. No cultivation has taken place since.

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Plot selection

The main premise of this study was to determine dominant species present within the seed bank of different plant communities (as presented by monocultures of field sedge, Nebraska sedge, Arctic Rush, and creeping wild rye) and to explore patterns between the seed bank composition with depth to ground water data and plant litter accumulation. Prior to this study, species composition data was gathered at Winters Ranch in 2012 and included 32 vegetation transects located at established ground water wells (instrumented with hobo data loggers to measure depth to ground water (Stringham unpublished data, 2012; Appendices B and G). These data were analyzed using a multivariate non-multi-dimensional scaling (NMS) analysis to identify dominant species associated with well sites. The analysis revealed that the locations that showed the most pronounced invasion by weeds were associated with wetland indicator species (FACW/OBL), including Nebraska sedge, Arctic rush, field sedge, and beardless wildrye (Stringham unpublished data, Appendix B). The data also indicated that two of the locations associated with Baltic rush and Nebraska sedge had no weeds in the overstory.

The NMS and a field observation map (Appendix A) were used to locate sample plots. Field investigations revealed repeating units of Nebraska sedge, Arctic rush, field sedge, and beardless wildrye) occurring in monocultures. In each sampling area, monocultures were paired with existing ground water monitoring wells. In addition, multiple historic irrigation ditches exist within the research area providing potential vectors for weed seed dispersal when spring runoff fills the ditches. Therefore, monocultures located within 10m of a historic ditch and associated with a groundwater monitoring well were included as sampling locations.

Field Methods

Collecting several small samples has been demonstrated to optimize the accuracy of estimates of seed numbers in the soil (Bigwood and Inouye, 1988). A total of 30 (composite of 5/m^2) samples were taken within specific monocultures at each well site (Appendix C). Seeds were collected in September of 2014 for seven monocultures across five well sites (wells 1,2,3,14,15) for a total of seven collection plots and 210 samples. Two well sites had two monocultures each. Seedbank sampling locations were randomly located within the monocultures associated with the groundwater monitoring wells located near the historic irrigation ditches. We only sampled locations if they contained at least 2m^2 of monoculture (no other species associates including standing dead/litter). Within the 2m^2 area, five sub-samples were taken 0.5 meters from the edge that were later combined to obtain a plot-level sample. Each subsample was taken with a soil auger 3 cm deep and 7.6 cm in diameter. Upon soil collection, all rhizomes, roots and any remaining live plant material was removed to ensure plants emergent in the seedbank study originated from seeds present in the seedbank. For each composite soil sample, location and litter depth were recorded.

Table 1.1. Soil samples for seed bioassays at each well site.

Well #	monoculture	Number of samples	Plot name (sites)
1	Field sedge	30	CP1
2	Nebraska sedge	30	CN2

2	Arctic rush	30	JA2
3	Wild rye	30	LT3
N14	Nebraska sedge	30	CN14
N14	Arctic rush	30	JA14
N15	Nebraska sedge	30	CN15
Total number of sub-samples		**210**	

Greenhouse Methods for Seed Bank Study

Bioassay sampling is used to identify the number of viable seeds in the seed bank without the need for laboriously sieving, collecting, and counting each seed. The viable seed bank was evaluated by direct germination following a cold stratification. This method has been demonstrated to accurately quantify the seed bank (Gross, 1990). After collection in September 2014, to break seed dormancy, each sample was wetted to field capacity and stored in a cold (<2 ºC) facility for 60 days. The samples were kept wet for 30 days, stirred, and then allowed to dry until December, 2014. No germination was noted during the cold stratification. Following seed stratification, soil samples were placed at a three-cm depth on top of sterile soil in individual 16 oz pots with drainage holes. Light cycles and temperature range in the greenhouse were similar to the field site germination and growth conditions until the bioassay was completed (6ºC at night and 22 ºC) during the day. The greenhouse temperature was then increased to 27ºC during the day to match site conditions for Washoe Valley. For each of the seven sampling plots, pots were randomly assigned to blocks within the greenhouse (Appendix D).

Seedlings were grown until proper identification. If seedlings were identifiable and pots were too crowded, seedlings were thinned. If seedlings were not identifiable, specimens were potted in separate containers and grown until seedlings could be properly identified. To control for seeds associated with the sterile potting medium, pots with just potting soil were randomly placed in the germination zone. There were a few species that germinated within the potting medium that were excluded from the analysis.

By October 2015, nearly all seed germination had occurred. Raw seedling counts were converted to seed density (seeds/m^2 depth). The density of the seeds (total per plot and for common species) in the soil was calculated based on the mean number of seeds per sample size calculated from all samples and then up-scaled to an area of m^2.

STATISTICAL OVERVIEW

In order to explore differences in diversity among communities, the species dataset was analyzed for species richness, evenness, and biodiversity. For biodiversity calculations we used the Simpson's diversity index because it slightly favors common species compared to Shannon's diversity and is a preferred index with sparse datasets. Biodiversity provides numbers of species and distribution among plots, but these measures do not provide information about specific species or groups of species occupying a similar niche (functional groups) that collectively influence ecosystem processes. Specific species analysis among plots was conducted using Hierarchical Cluster Analysis. To explore differences between functional groups and plots, the species dataset was categorized by *functional group*. The categories included exotics annuals, native perennials, a category combining wetland indicator species upland/facultative species, a category combining facultative wetland/OBL species, and a category that included species associated with the historic reference community for Wet Meadow 14+” P.Z. R026XY054NV. Analysis of variance (ANOVA) was used to detect the effects of plot on functional group using JMP®, Version 12.0 (SAS Institute Inc., Cary, NC,2007).

To explore if specific species and functional groups within wetlands could be predicted by environmental factors, the data was first explored for pattern between seedbank composition and community type and environmental variables using multivariate analysis in PC-ORD (version 6.0; MjM software, Gleneden Beach, Oregon). Multiple regression analyses were performed to explore correlations between environmental variables and seedling numbers within each functional group using the functional groups as the response variables and depth to ground water, and litter depth as predictor variables. The depth to ground water categories included the five-year annual average value and DTW in March (when seedlings are emerging). Simple linear regressions were used to predict litter height and specific species abundance. These tests were performed using all of the sub-samples and predictor variable values and then using averages of functional group abundance and average litter by plot. A plot is defined by specific host monoculture at a specific well location (Table 1.1). The data were analyzed in both untransformed and log transformed format. Data transformation did not yield different results so untransformed data were used for all tests. In evaluating results, P values less than 0.05 were considered significant. Analyses for species questions are explained below.

1. How does seed bank vary among plots?

a. How does diversity vary at the plot level?

The first set of analysis included all species in the dataset. For each plot we calculated species richness S (number of species per experimental unit), evenness (E) = H/species richness, and Simpson's diversity index in PC ORD. The Simpson diversity index indicates dominance because it gives more weight to common or dominant species. In this case, a few rare species with only a few representatives will not affect the diversity.

b. Do species vary among plots?

Because of the sparsity of the seed bank dataset, this question was explored using hierarchical cluster analysis (HCA) in PC-ORD that allows the classification of sample units to groups based on the level of similarity and constancy throughout the dataset. Rare species (species with less than <1% occurrence in the data set) were excluded from the analysis. The HCA was done using the group average linkage method and Sorenson (Bray-Curtis) distance measure. The number of clusters to present was chosen based on the number that produced the highest average maximum indicator value, based on indicator species analysis (McCune and Grace, 2002), and also had significant difference between clusters based on multi-response permutation procedure (MRPP). Values of A larger than 0.3 are considered to represent high effect sizes.

c. How do functional groups vary among plots?

Each species was assigned to a functional group (Appendix F) including: exotics, native perennials, FACW/OBL, FAC/UPL, and species historically associated with the Rangeland Ecological Site Description (ESD) Wet Meadow 14+ P.Z. (R026XY054NV DECE) in western Nevada for a total of five functional groups. Once aggregated, functional groups were analyzed using one-way ANOVA to detect effects of plot and Tukey's HSD post hoc was run to test for differences between plots.

2. How do functional groups and specific species, relate to environmental conditions (litter and depth to ground water)?

Depth to water categories (DTW) (Appendix E) and litter height were used as predictor variables. To test the hypotheses/assumptions, data were analyzed using the general linear model procedures (either simple linear regression or ANOVA) in JMP, version 12 to test the differences in the numbers of exotic, cheatgrass, late seral, and *Deschampsia* seedlings with litter depth and DTW. Lastly, we ran a Principal Components Analysis (PCA) to explore pattern and confirm results.

RESULTS

A total of 2,416 seedlings and 33 plant taxa were observed in the seed bank: eight native perennial bunchgrasses, 15 native forbs, four annual exotic grasses, and six herbaceous exotic species. The average number of seedlings per plot was 392 (Table 1.2). The most common seedlings included annual exotic grasses *Bromus tectorum* (16%), *B.arvensis* (6%), and *Apera interrupta* (6%) (Appendix F)*.* One of the most common native seeds in the bioassay was *Deschampsia cespitosum* (13% of total bioassay). However, this species was not growing at any of the plots. Other common native seeds in the seed bank assay included willow herb (*Epilobium ciliatum*), monkey flower (*Mimulus guttatus*), and bluegrass (*Poa* compressa) (composite 18% of bioassay). None of these species were dominant vegetation at Winters Ranch (Stringham unpublished data, collected summer 2012). Seedlings that were not as common (5% collectively within the assay) included Nebraska sedge (*Carex nebrascensis*), Arctic rush (*Juncus arcticus*), and field sedge (*C. praegracilis*). However, these species generally propagate vegetatively particularly in a grazed system. These species are the dominant vegetation and served as vegetation monocultures from which soil samples were taken.

1. How does seed bank vary among communities?

a. How does diversity vary among plots?

Table 1.2 shows the diversity among all the plots, using the S (species richness), E (evenness), and D (Simpson’s diversity) indices.

Table 1.2. Biodiversity of plant seedlings per plot

Plots	Sum	S	E	D
Arctic rush well 14 (JA14)	652	14	0.62	0.44
Arctic rush well 2 (JA2)	153	15	0.49	0.32
Nebraska sedge well 2 (CN2)	309	13	0.68	0.48
Nebraska sedge well 14 (CN14)	519	17	0.80	0.57
Field sedge well 1 (CP1)	239	12	0.61	0.40
Wild rye well 3 (LT3)	529	12	0.63	0.38
Nebraska sedge well 15 (CN15)	322	14	0.60	0.37
Average	392	13.9	0.63	0.42

S= species richness (the number of species among plots).
E= evenness (equitability or proportion of species among plots)
D=Simpson's index of diversity for an infinite population.

The biodiversity between plots is relatively similar (Table 1.2). While the range of species richness is between 12 and 17 species, the average distribution of all species across all sub-samples per plot are similar with the exceptions of JA2 as indicated by lower evenness value (E=.49) and CN14 with a higher evenness value (E=.80). The JA14 shows a higher (sum of 652) number of seedlings and species richness of 14, but those seedlings are evenly distributed throughout the sampling plots when compared to average of all plots. The Simpson's diversity index reflects both species richness and evenness with 1 being infinite diversity. The data demonstrates the highest biodiversity among plots at CN2, CN14 and JA14 and the lowest biodiversity at JA2 and CN15.

b. Do species vary among plots?

Figure 1.1 HCA of species within plots. Used group average linkage method and Sorenson distance metric. Four clusters had the highest average maximum indicator value, based on indicator species analysis (McCune and Grace 2002). Only plots with significant correlations (p>.05) with clusters of species are presented on figure.

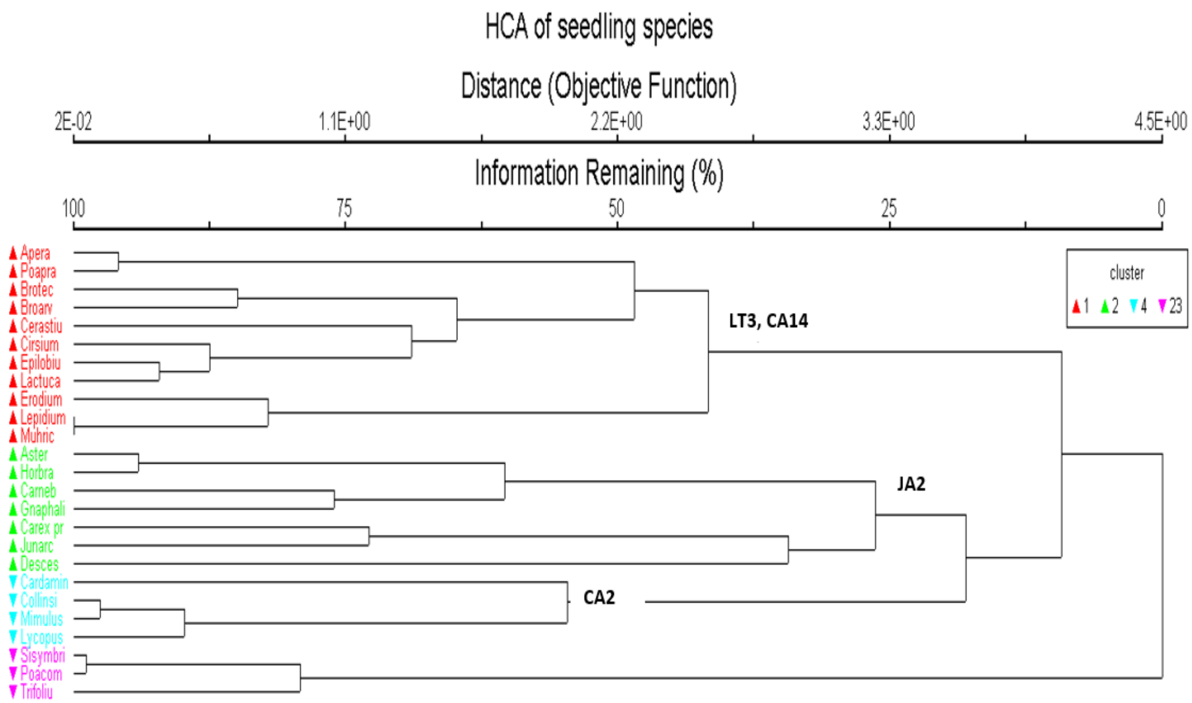


Table 1.3. Indicator species analysis based on four groups. Maximum group refers to groupings from HCA from Figure 1.1. P values are from a Monte Carlo test of significance of observed maximum indicator values compared to mean value from randomized groups.

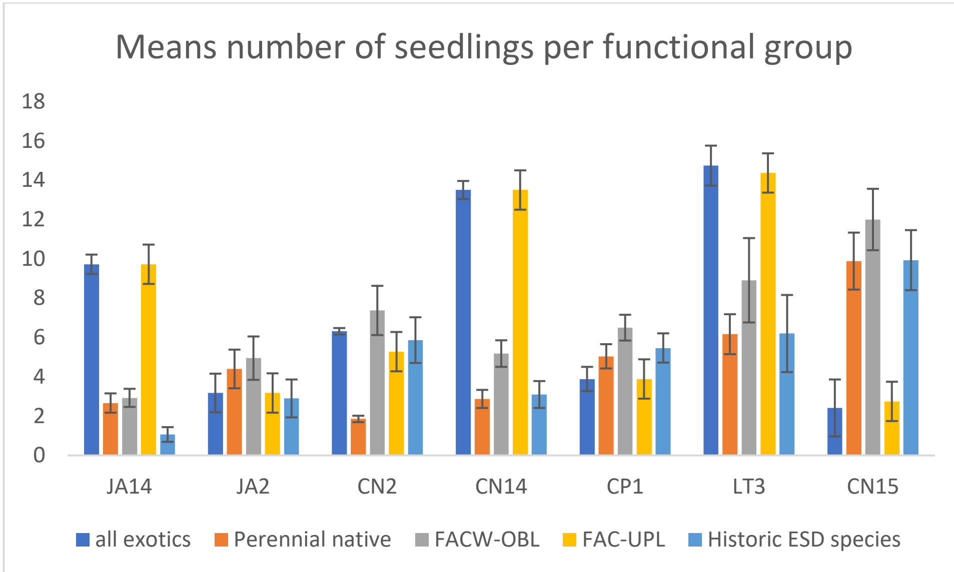
Plot	Maxgrp	P value
Arctic rush well 14 (JA14)	23	0.2484
Arctic rush well 2 (JA2)	2	0.0378
Nebraska sedge well 2 (CN2)	4	0.0006
Nebraska sedge well 14 (CN14)	1	0.0008
Field sedge well 1 (CP1)	2	0.3413
Wild rye well 3 (LT3)	1	0.0222
Nebraska sedge well 15 (CN15)	2	0.1532

Cluster analysis indicates four groups that are significantly distinct (Figure 1.1 and Table 1.3). Group 1 (red) is significantly associated with LT3 in the creeping wildrye (*Leymus triticoides*) monoculture and CN14 in the Nebraska sedge monoculture. These plots are dominated by drier exotic winter annual species such as silky bentgrass (*Apera interrupta*), cheatgrass (*Bromus tectorum*), and prickly wire lettuce (*Lactuca serriola*). Group 2 (green) is significantly correlated with JA2 and was dominated by perennial C3 wetland species including sedge (*Carex nebrascensis* and *C. praegracilis*) and tufted hairgrass (*Deschampsia cespitosum*). Group 4 (blue), significantly correlated with CN2, is presented by a mixture of native and non-native forbs including water hore-hound (*Lycopus americanus*) and blue-eyed Mary (*Collinsia parviflora*). Group 23 consists of weedy exotic species tumble mustard (*Sisymbrium altisissimum),* perennial wetland graminoid Canadian bluegrass (*Poa compressa)*, and clover (*Trifolium* sp.) and was weakly associated with the JA14, significance (p= 0.2484).

c. How do functional groups vary at the plot level?

Plot level means indicate a higher number of exotic seedlings species at the *Carex nebrascensis* and *Juncus arcticus* plots at Well 14 (CN14, JA14) and the *Leymus triticoides* plot at Well 3 (LT3) and a lower number at plot CN15 (Figure 1.2). Within the perennial plant functional group, means covered a broad range with the lowest number of perennial seedlings in CN2 and the highest numbers at CN15. JA2, CP1, and CN2 had proportionally lower numbers of all functional groups. CN2 and CN15 displayed the highest number of historic species than the other plots.

Figure 1.2. Mean number of seedlings and SE by functional group per plot. Exotic upland seedlings were most prevalent at wells 3 and 14 whereas perennial late seral species were greatest at well 15. Arctic rush well 14 (JA14), Arctic rush well 2 (JA2), Nebraska sedge well 2 (CN2), Nebraska sedge well 14 (CN14), Field sedge well 1 (CP1), Wild rye well 3 (LT3) Nebraska sedge well 15 (CN15).



2. Correlations between species and litter depth and depth to groundwater.

a. Upland/FAC and exotics

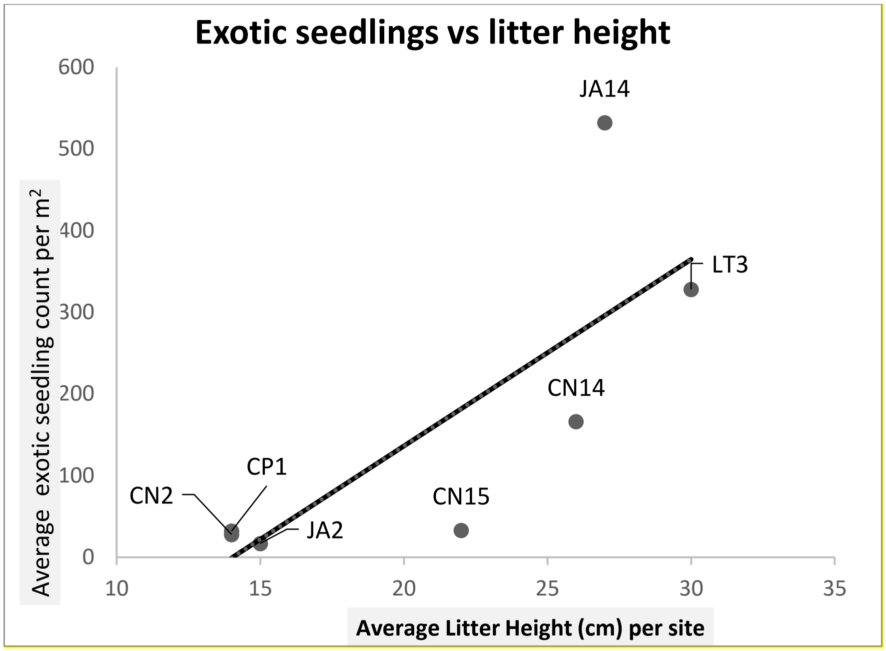
Litter height exhibited a positive, significant relationship with both exotic and FAC/Upland functional group seedlings (Table 1.4), but there was no significant relationship between DTW and exotic or FAC/upland seedlings. Results from the PCA demonstrated similar relationships (Appendix G).

Table 1.4. Results of mixed model of exotic and UPL/FAC functional groups and environmental variables, n=210

Exotics	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
litter height	0.6179123	0.152399	4.05	<.0001*
annual average 2012-2017	0.1051349	0.099039	1.06	0.2897
March (2012-2017)	-0.09722	0.081999	-1.19	0.2371
FAC/UPL	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
litter height	0.6829646	0.151201	4.52	<.0001*
annual average 2012-2017	0.073902	0.098259	0.75	0.4528
March (2012-2017)	-0.073316	0.081354	-0.90	0.3685

The model confirmed that exotic seedling numbers increase with increasing litter depth (p=0.038). Figure 1.3 portrays the relationship between average litter height per plot and average exotic seedling counts per plot. For every 1 cm increase in litter height seedling density increases by 22.8 seedlings per m^2. If scaled up to an acre at the current height at well 3 for example, 30 cm equals 49,210 exotic seeds/acre.

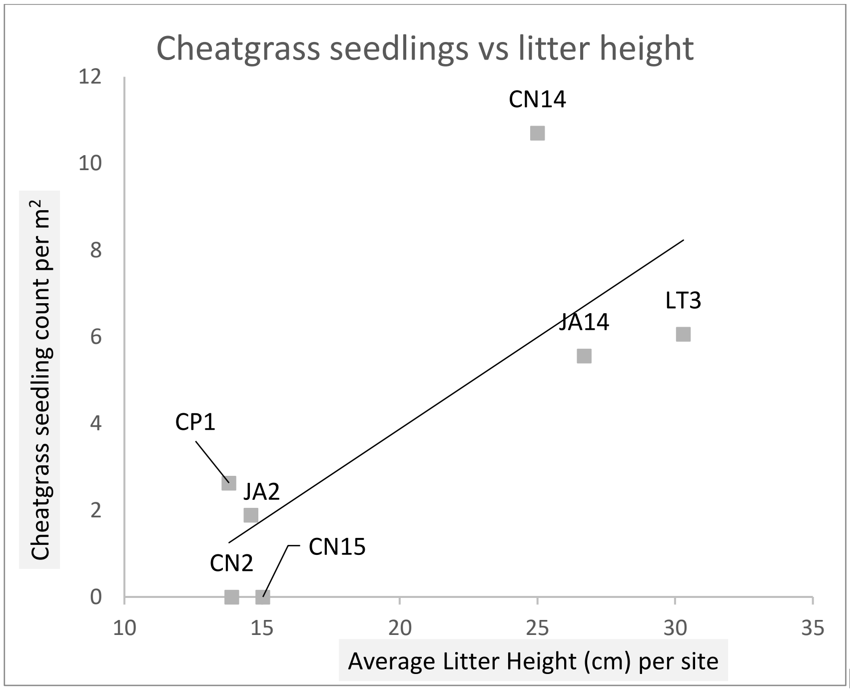
Figure 1.3. Exotic seedlings per m^2 in relation to average litter height (cm). Arctic rush well 14 (JA14), Arctic rush well 2 (JA2), Nebraska sedge well 2 (CN2), Nebraska sedge well 14 (CN14), Field sedge well 1 (CP1), Wild rye well 3 (LT3) Nebraska sedge well 15 (CN15).



b. Cheatgrass (*Bromus tectorum*)

The model showed that cheatgrass seedling numbers increase with increasing litter depth ($p=0.04$). Figure 1.4 portrays the relationship between average litter height per plot and average cheatgrass seedling counts per plot. For every 1 cm increase in litter height seedling density increased by 0.4 seeds per m^2. Regression analysis showed no significant correlations between March DTW and cheatgrass ($p=0.36$) or Annual DTW and cheatgrass ($p=0.35$).

Figure 1.4. Cheatgrass seedlings per plot in relation to average litter height (cm). Arctic rush well 14 (JA14), Arctic rush well 2 (JA2), Nebraska sedge well 2 (CN2), Nebraska sedge well 14 (CN14), Field sedge well 1 (CP1), Wild rye well 3 (LT3) Nebraska sedge well 15 (CN15).



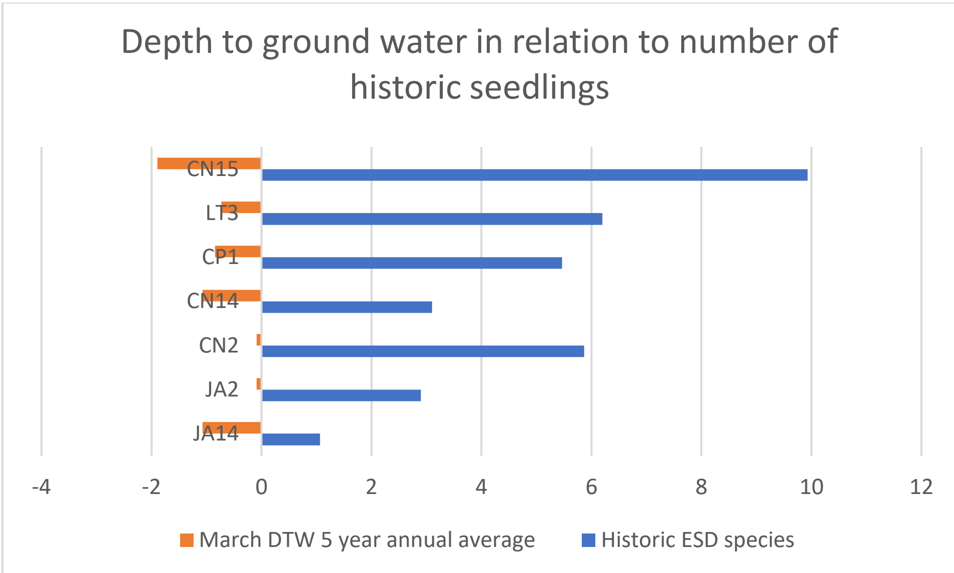
c. Perennial natives, historic species, and wetland (FACW/OBL) species

Late seral species seedling numbers had a significant relationship with both DTW levels (5-year average 2012-2017; Table 1.5). However, seedlings were negatively correlated with the average annual depth to ground water and positively correlated with the average March water table (Figure 1.5). The PCA demonstrated similar results (Appendix H). These results are opposite to those of the exotic/DTW relationship demonstrating that late seral seedlings prefer drier conditions in the spring and wetter conditions in March. This result is likely typical of agricultural wetlands that are drying out due to a decrease in irrigation or ground water pumping. Late seral species had no significant relationship with litter.

Table 1.5. Results of the mixed model of Perennial native, FACW/OBL, and Historic/Late seral functional groups and environmental variables, n=210

Perennial native	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
annual average 2012-2017 (cm)	-0.145103	0.044615	-3.25	0.0013*
March (2012-2017) cm	0.1558518	0.036939	4.22	<.0001*
litter height	-0.05764	0.068653	-0.84	0.4021
FACW/OBL	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
annual average 2012-2017 (cm)	-0.178092	0.065941	-2.70	0.0075*
March (2012-2017) cm	0.1744387	0.054596	3.20	0.0016*
litter height	-0.055822	0.101469	-0.55	0.5828
Historic/Late seral	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
annual average 2012-2017 (cm)	-0.259841	0.070218	-3.70	0.0003*
March (2012-2017) cm	0.2361214	0.058137	4.06	<.0001*
litter height	0.1494043	0.108051	1.38	0.1682

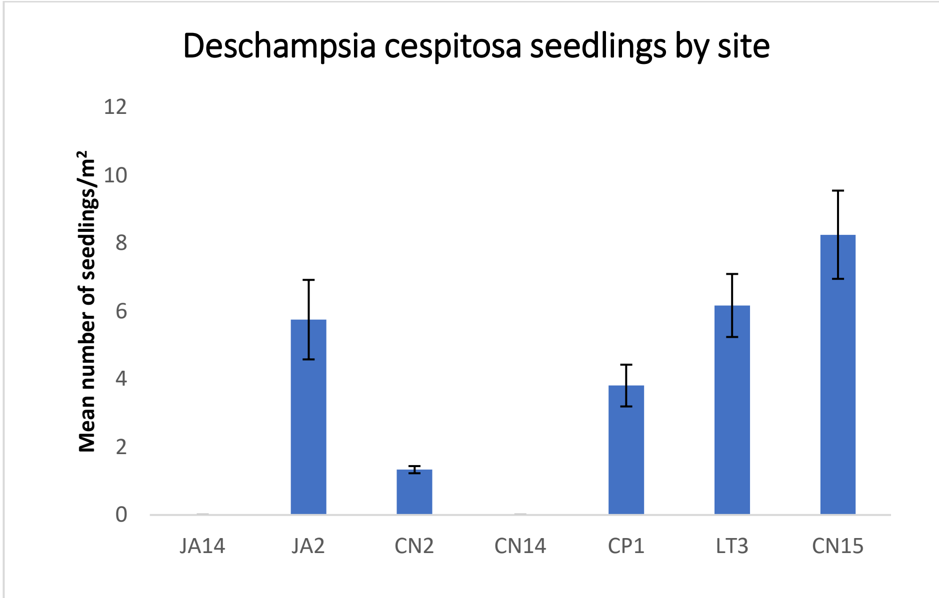
Figure 1.5. Mean number of historic species m^2 in relation to 5-year (2012-2017) March average (m). Arctic rush well 14 (JA14), Arctic rush well 2 (JA2), Nebraska sedge well 2 (CN2), Nebraska sedge well 14 (CN14), Field sedge well 1 (CP1), Wild rye well 3 (LT3) Nebraska sedge well 15 (CN15).



d. *Deschampsia cespitosa*

Study results from the bioassay indicated that a major component from the reference communities as described in the NRCS ecological site descriptions (USDA, 2003) ESD were present within the seed bank. This species was not found in the aboveground vegetation however. Similar to the results for late seral species, results revealed the highest number of *D. cespitosa* at wells 15 and 3. No seedlings were present at the plots that had the highest occurrences of weeds (both Arctic rush and Nebraska sedge monocultures at well 14. *Deschampsia cespitosa* had no significant relationship with either depth to groundwater level or litter.

Figure 1.6. Mean and SE number of Deschampsia seedlings per sample.



DISCUSSION

Seedbank characteristics

Despite the similarity in biodiversity of the seed banks within monocultures and between plots, we found significant differences between the density of seedlings and types of species present. The plots dominated by exotic species had a higher seed density while the plots dominated by late seral species had lower seed densities. This is likely because exotic species have a reproductive strategy that select for traits associated with a higher seedling establishment success rate rather than late seral species that select for traits associated for dispersal in time or space (Hermy 1999). Additionally, as is the case with an agricultural wetland, Maron and Gardner (2000) found that stable mowed or grazed communities with limited safe sites, favored species investing in seedling competitive ability or clonal reproduction.

Plot level means indicate a higher number of exotic winter annual seedlings species at wells 14 and 3, while late seral cool season species dominated at wells 2 and 15. This finding is consistent with studies that report locations subjected to stress such as droughts will select for traits associated with higher seedling establishment (Hermy 1999). One of the main sources of stress or stability at the study is likely water related (drought, lack of irrigation, ground water depletion or water availability). Our results indicate a positive significant relationship between late seral species and depth to ground water in March, and a negative significant relationship for the annual average indicating that DTW is an important factor in site stability as indicated by the presence of late seral species. Though there was no significant correlation between exotic species and DTW, a larger sample size with more well sites would likely present a relationship opposite to that of late seral species, meaning a negative relationship with DTW in March and a positive relationship with the overall average.

Regardless of the mechanism of stress or biodiversity among plots, we discovered that the *type* of exotic species expressed in the seed bank data at Winters Ranch were winter annual species while the *type* of late seral species were predominantly cool season species such as *Deschampsia cespitosa*. In terms of management this is important because winter annual weeds are significant competitors with cool season species in the early spring because they have the ability to overwinter as small seedlings and initiate significant growth during the early spring. They have the ability to survive and grow during times of the year when environmental conditions particularly temperature are not favorable for the development of other plant species (Radosevich et al., 1997; Creech et al., 2007b). For example, the minimum germination temperature for cheatgrass is between -1 and 1 degree 1°C (Harris, 1967 and Thill et al. 1980) whereas the production of cool season grasses had to exceed 10°C in the spring for emergence of new shoots to begin (Ratliff and Westfall,1992). These data suggest that based on temperature alone, the winter annuals at Winters Ranch would have a competitive advantage over the C3 perennials species.

The weather data for the study site shows a mean average of 1.1 C in March which is cooler than is required for growth for cool season grasses, but not for winter annuals. However, the one competitive advantage C3 species might have, particularly FACW/OBL species would be morphological adaptions (aerenchyma cells) for inundated soils. Cheatgrass grows under a normal range of conditions to a soil moisture of -1.5 MPa (fairly dry) (Evans and Young, 1970). In this study, although there was no direct correlation between DTW and density possibly due to the low sample size, exotic seedlings had the highest abundance at sites with a water table at least 100 cm (five-year average) below the surface for the entire growing season suggesting that sites that are inundated in March may not suit germination requirements for cheatgrass giving C3 FACW/OBL and chance to compete.

Litter accumulation and exotic seeds

The results of our seed bank study demonstrated that litter height was positively correlated with exotic seedlings, specifically 49,210 seedlings per one cm increase in litter height/acre. In addition, cheatgrass seeds were positively correlated with litter height consistent with earlier research suggesting cheatgrass prefer litter cover to bare soil to geminate (Evans and Young 1987b)

The wetland site at Winters Ranch was historically grazed and irrigated until 10 years prior to this study. Since then, the species composition dominated by highly lignified species and hydrologic alteration (discontinuing irrigation, ground water diversion, or climate change) has likely decreased the rate of decomposition. Studies suggest that in areas where hydrology is altered, flood-pulsed hydrology may be the missing factor that can promote aquatic dispersal and other landscape-level processes such as decomposition in floodplain restoration projects (Middleton, 2002). Though the rate of decomposition in relation to DTW was not tested during the study, the accumulation of standing dead litter has accumulated to a depth between 14-30 cm in the study area suggesting decomposition is retarded. In addition, during most of the four-year study, the study site was in a drought and not inundated at the surface suggesting that the lack of decomposition was not due to poor aeration but due to moisture limitations of the decomposer community as suggested by Beard (1973). This hypothesis needs to be further tested at the study site by comparing the decomposition rates of different dominant species within different soil moisture regimes associated with varying DTW levels.

In areas with a shorter litter depth, late seral seeds were more abundant than exotic seeds. The knowledge of the types of dominant species in the seed bank (late seral species and winter annuals) and their growth preferences (shallower litter in wetter plots in the spring vs. deeper litter and drier soils in the spring) allows us to infer that higher soil moisture or a shallower depth to ground water can reduce litter accumulation which in turn supports decomposition, resistance to weed invasion, and a stable regeneration of late seral seeds.

Identification of hydrologically impacted wetlands and development of weed management plans focused on aboveground biomass control has important implications for determining the successional trajectory of the wetland.

Longevity of seeds in wetlands, species missing, and Deschampsia cespitosa

A main objective of this study was to identify the types of late seral species in the seed bank, identify those that may be missing from the aboveground vegetation, and to speculate as to why those species are missing. These data could be used to improve the species characteristics for the Rangeland Ecological Site Description (ESD), Wet Meadow 14+ P.Z. (R026XY054NV) and inform a state and transition model.

One of the most important results of the individual species analysis was that dominant species in the seedbank do not reflect above ground vegetation. For example, *Deschampsia cespitosa* was one of the most dominant species in the bioassay, despite being absent from the above ground vegetation in all but one well site. Most authors agree that restoration based on the seed bank is only possible at sites that were degraded less than 5 years ago. One exception are marsh species that are adapted to recurring draw-down cycles (van der Valk & Davis 1978). Research on seed longevity has suggested that marsh species, including herbaceous species (Middleton 2003) produce seeds that can remain viable for a long time. Seeds of these species remain viable in the soil awaiting recurring suitable conditions for germination in a flooding and draw down cycle. The frequency of flooding could range from daily and regular, such as in salt marshes, to decades and very unpredictable (Egan & Ungar 2000). Studies onseed viability and longevity for *Deschampsia* are inconclusive. Studies by Chambers (1989) reported high variability of seed viability for *Deschampsia cespitosa* attributed to the severe and unpredictable nature of the environment. The absence of *Deschampsia* in the aboveground vegetation would suggest that either the seed is long-lived or uniformly transported from off site. A study by Verheyen and Hermy (2000), suggests however that *Deschampsia cespitosa* lacks adaptations for long-distance dispersal indicating the study site at Winters Ranch may have once been dominated by *Deschampsia*.

This species was found in all but one well site (well site 14). This site has a similar range of soil characteristics, DTW, species composition, and litter depth. It is likely that the legacy effects eliminated the species from this area supporting the research by Weinhold and van der Valk,1989 and Hutchings and Booth, 1996, suggesting that after cultivation or grazing ceases, important structural components of vegetation that used to be dominant may not spontaneously re-emerge.

CONCLUSION

Our study showed that there was little correlation between community composition and composition of the seed bank so it is unclear seedbank composition is an accurate predictor for restoration success. Still, some sampling plots revealed a seedbank dominated by late seral species, suggesting that some areas have the potential to return to a late seral state. Winters Ranch has remained fallow for 12 years. Drastic changes in hydrology (lack of irrigation, diversions, ground water pumping) and lack of biomass removal has resulted in the accumulation of litter and unexpected weed infestations. These areas will require the most effort to restore.

Management suggestions and implications

The wet meadows at Winters Ranch are currently dominated by monocultures of a few select species. Some of the areas are maintaining a seedbank and species composition of late seral species, however, these areas are dominated by late seral species but the seedbank is dominated by exotic annuals. An additional concern is the lack of late seral- species diversity on the landscape. This is a concern because the lack of diversity above ground may reflect diversity below ground. Different species occupy different niches in the rhizospere that support microbial activity and nutrient exchange throughout the profile.

Although, all areas require some level of input through the introduction of a more diverse species composition, the areas of deep litter accumulation will also require reconditioning by removing excessive amounts of litter and standing dead plant materials to avoid dominance by exotic annuals. To date, there are several potential management techniques that could be used. Knowledge of the seedbank and the potential risks involved with implementing specific techniques are discussed below.

Fire

Fire is a common tool used for biomass management. The areas with less litter and a dominance of late seral seedlings would likely benefit from light intensity fire because (assuming seeds remain viable) a more open canopy may encourage the germination of dormant late seral species such as *Deschampsia*. The remaining dominant species, (Nebraska sedge, Baltic rush, and wild rye,) are generally top-killed by fire, but root crowns usually survive all but the most severe fires. Assuming the layer of standing dead/litter does not create a fire too intense for the plant to sustain, individual plants will likely benefit.

The areas with high levels of standing dead and litter are likely the most vulnerable to the effects of fire. The remaining vegetation would be at great risk from a potentially higher intensity fire associated with a thick layer of litter/fine fuel. It is likely that the late seral species that do remain would not survive and would not be able to compete with weed emerging seedlings. Most importantly, the seedbank in these areas is dominated by cheatgrass seeds. The effects of fire on cheatgrass is widely studied. Though there is evidence that cheatgrass seeds are reduced following high intensity fire (Young et al. 1969), there is an abundance of evidence suggesting larger more frequent fires associated with cheatgrass in the Great Basin has caused a reduction in rangeland productivity, significant changes in species richness, vegetation composition, structure, wildlife habitat, and ecosystem processes (Harrison et al. 2003 and Knapp 1996

Grazing and mowing to improve species composition

Grazing is likely the most feasible management tool for reducing thatch and influencing a desirable species composition. However, there are several risks associated with grazing particularly if grazing is preventing recovery of key species which often results in a community of less palatable species. Therefore, understanding the mechanisms of recovery for specific species following grazing are crucial for maintaining the site.

When the photosynthetic surface of the leaf is removed, the photosynthetic supply and source that generates and transports the carbohydrates to the whole plant is interrupted. To compensate, plants allocate carbohydrates stored in the roots for repair and shoot development to again restore the photosynthetic pump (Briske 1991). If root reserves are repeatedly depleted from multiple defoliations, the effects to the overall production and plant community could be reduced. In a continuously grazed system, preferred species are generally grazed multiple times in a season and cannot fully recover. Therefore, when developing a grazing plan, allowing for proper recovery of key plant species is essential. This can be achieved by implementing a grazing system that incorporates knowledge of plant species response to frequency, timing, and intensity of defoliation. An additional side effect of grazing in wet meadow systems is that it may result in soil compaction, adversely impacting soil physical properties.

Mowing may be an alternative to grazing for biomass reduction. Although mowing may be logistically easier, and may not adversely affect soil structure, it is not a substitution for grazing. It is generally thought that large herbivores can serve an important role in decomposition, accelerating nutrient cycling (Holland et al. 1992; Zimov et al. 1995, and Sirotnak and Huntly 2000) as a result of incorporation of ruminant fluid, feces, and urine from hoof action. For these reasons, grazing is recommended over mowing but should be implemented at a time when the soil is not inundated and susceptible to the sheer forces of hoof action. Using high intensity grazing such as mob grazing where the animal density is high enough to force the consumption of undesirable species and biomass when soils are dry is recommended.

Sustainable management practices imply that the land be managed in a manner that maintains the functions and processes of the landscape. If wetland systems which have served the purpose of agriculture are to regenerate, management must aim toward identifying dominant species requirements and their function in the system, and thresholds that encourage sustainability.

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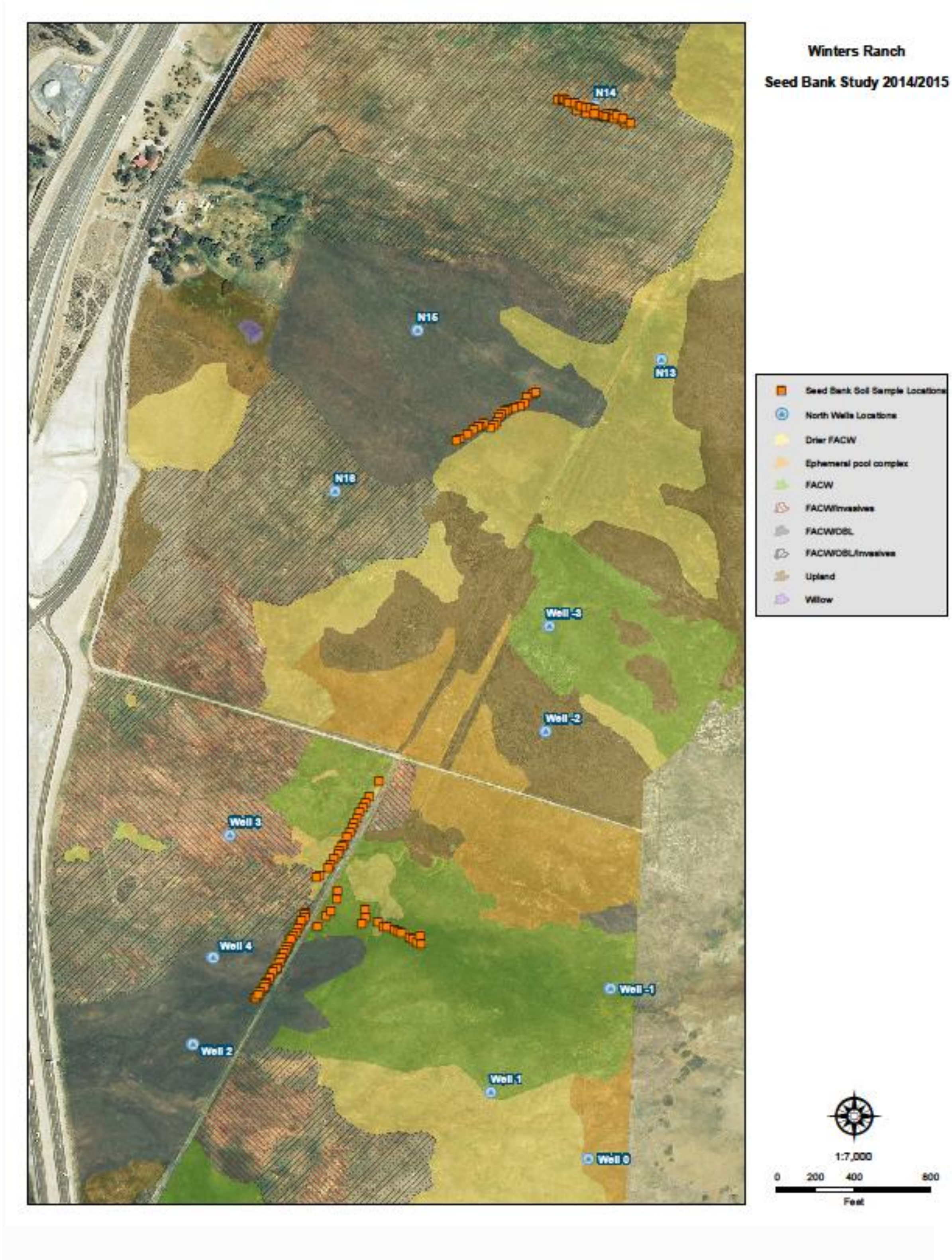
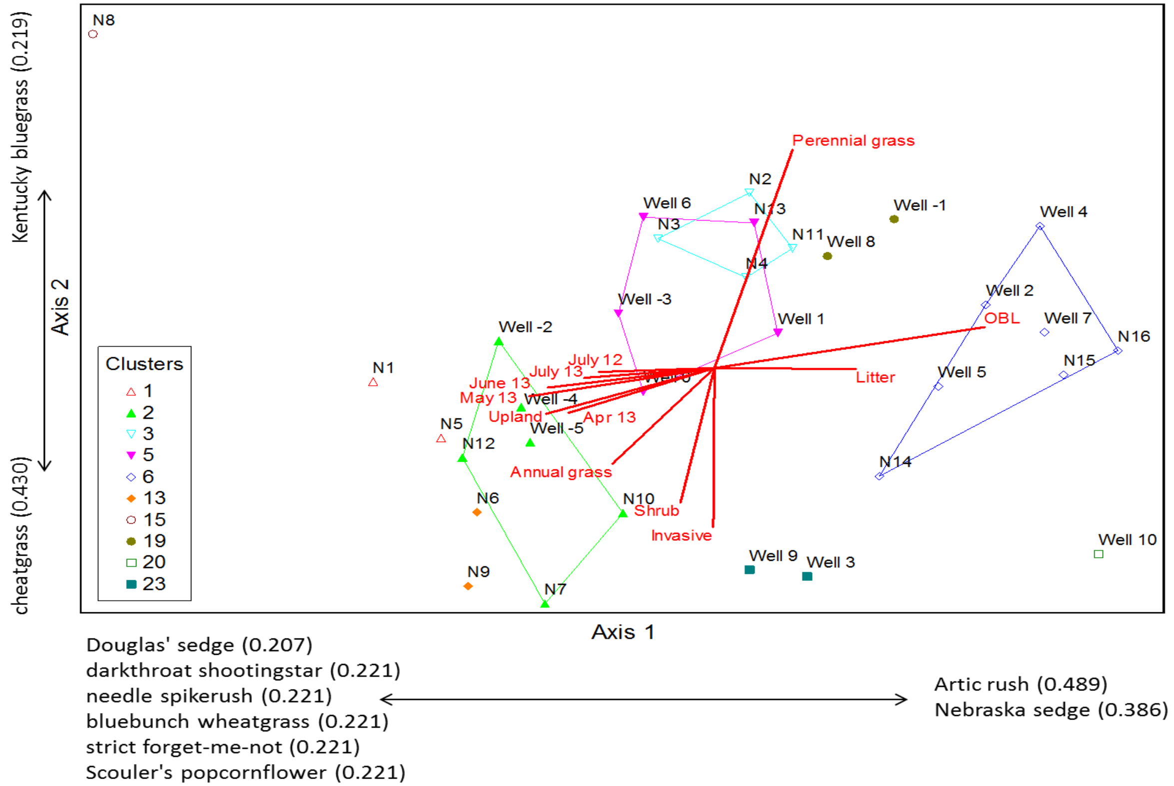
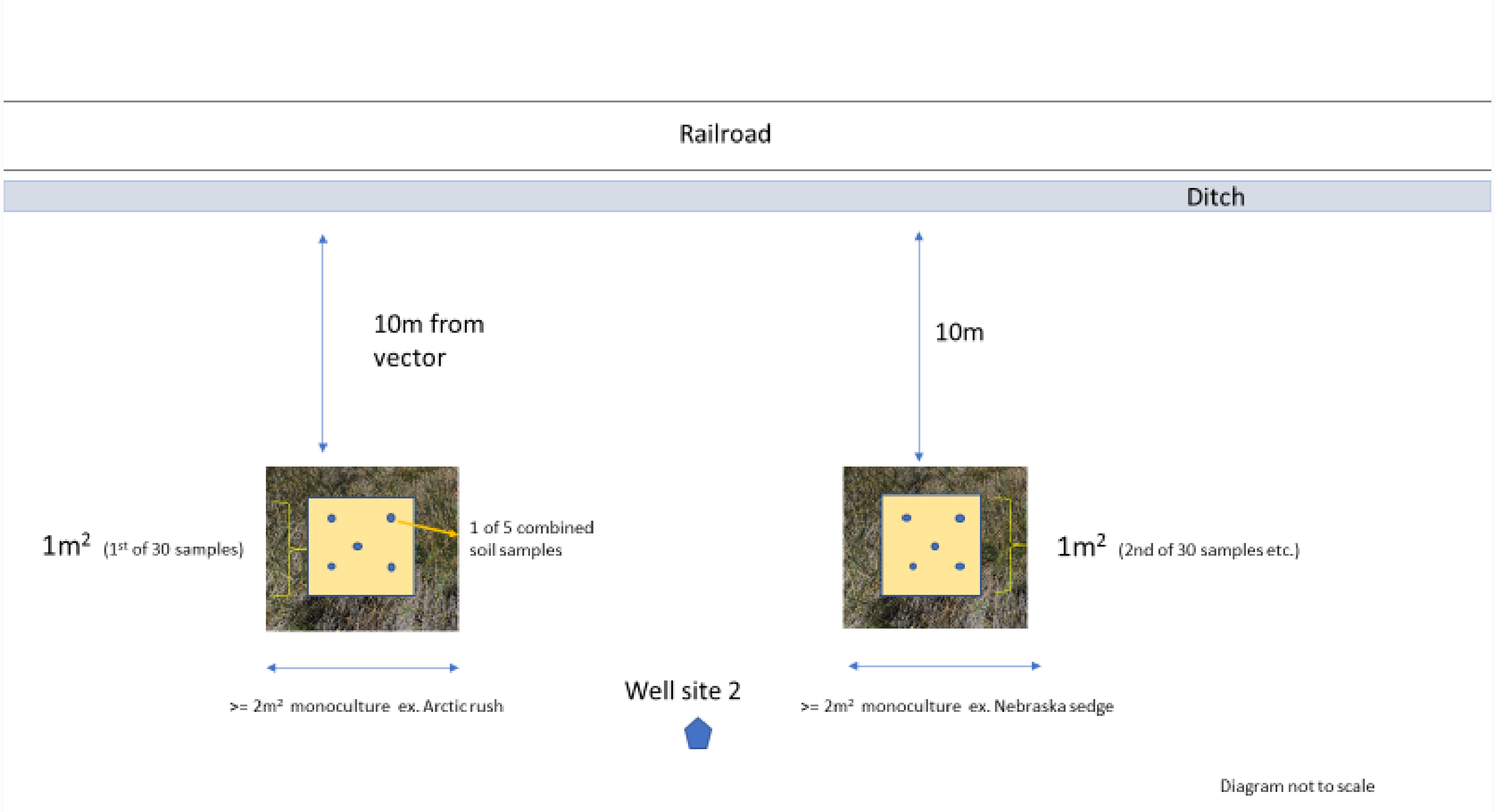
APPENDICES



Appendix A. Study site and soil sample locations



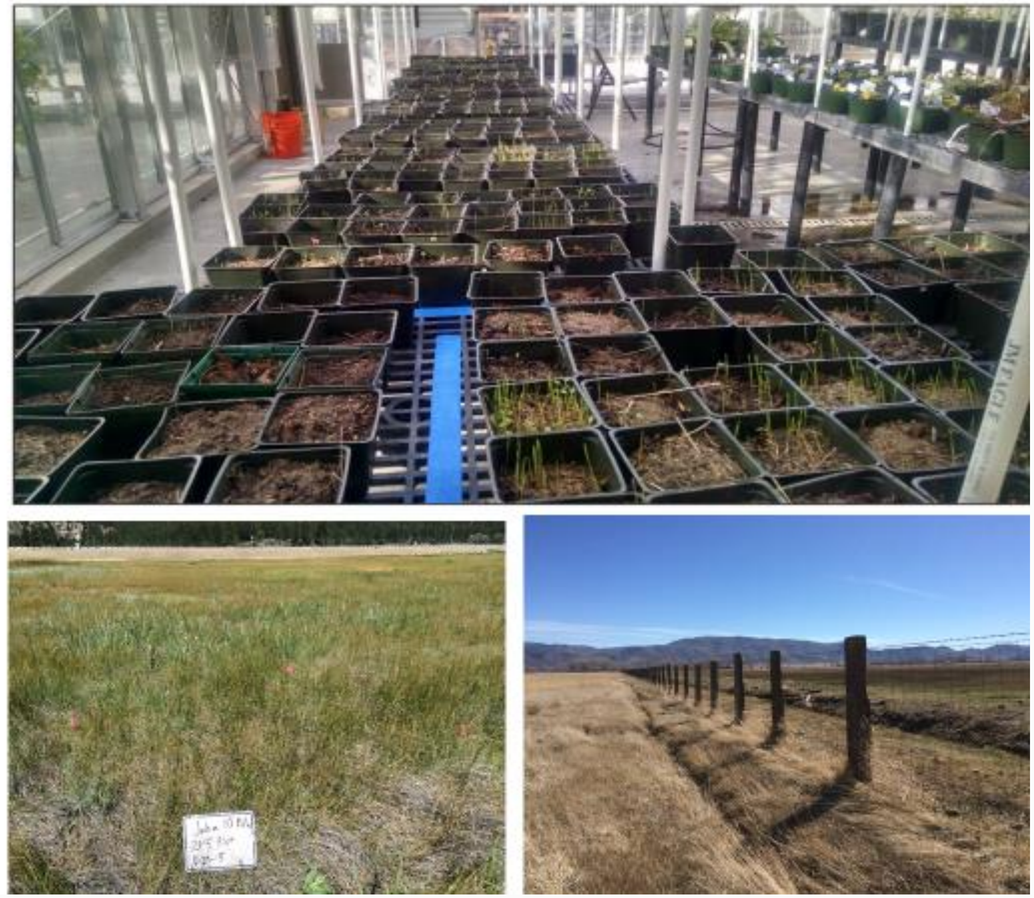
Appendix B. Nonmetric multidimensional scaling (NMS) analysis, *using Sorenson (Bray-Curtis) distance measure was run to ordinate wells along component axes. The proportion of variance represent by axis 1 0.507, with axis 2 representing an additional 0.126, and axis 3 an addition 0.128. Stress for the 3 axis ordination was 9.60. Red lines show plot characteristics (cover of functional groups, invasive categories, and wetland categories, depth to water (April through July monthly average, and litter) correlated with the ordination axes with an r^2 of at least 0.2. The species most strongly correlated with axis 1 and 2 (r^2>0.2) are also labeled. The ordination demonstrates a clear separation between wetter plots (on the right, cluster 6) and drier, upland plots on the left at deeper wells (cluster 2).*



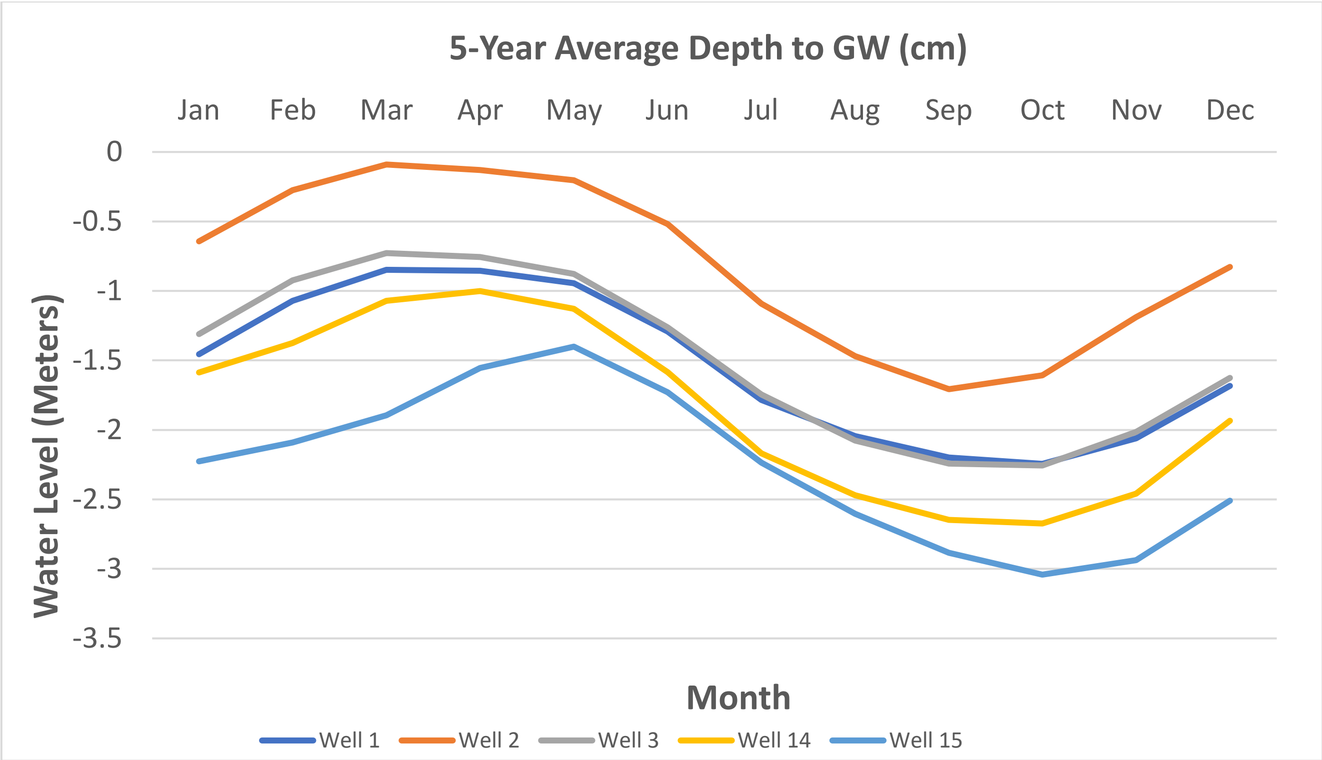
Appendix C. Experimental Design

Seed Bank assay

- Collected 30 soil samples from monocultures along ditches
- Monocultures
  - Creeping wild rye
  - Field sedge
  - Nebraska sedge
  - Baltic rush



Appendix D. Photos of seed bank study



Appendix E. Hydrograph of five-year average of depth to ground water (m)

The hydrograph in Appendix E illustrates that the average (2012-2017) change in depth to ground water is relatively proportional in all of the wells. The annual average and DTW in March (when seedlings are emerging) were used to explore relationships between litter depth and DTW. Well 2 has a water table close to the surface and is sometimes inundated through much of the early growing season. Wells 1, 3, 14, and 15 are 50-75 cm deeper throughout the growing season. All wells rapidly recede beginning in early June to a depth below the permanent wilting point where the matric water adsorbed by soil particles is held so tightly it cannot be removed by plant root cells.

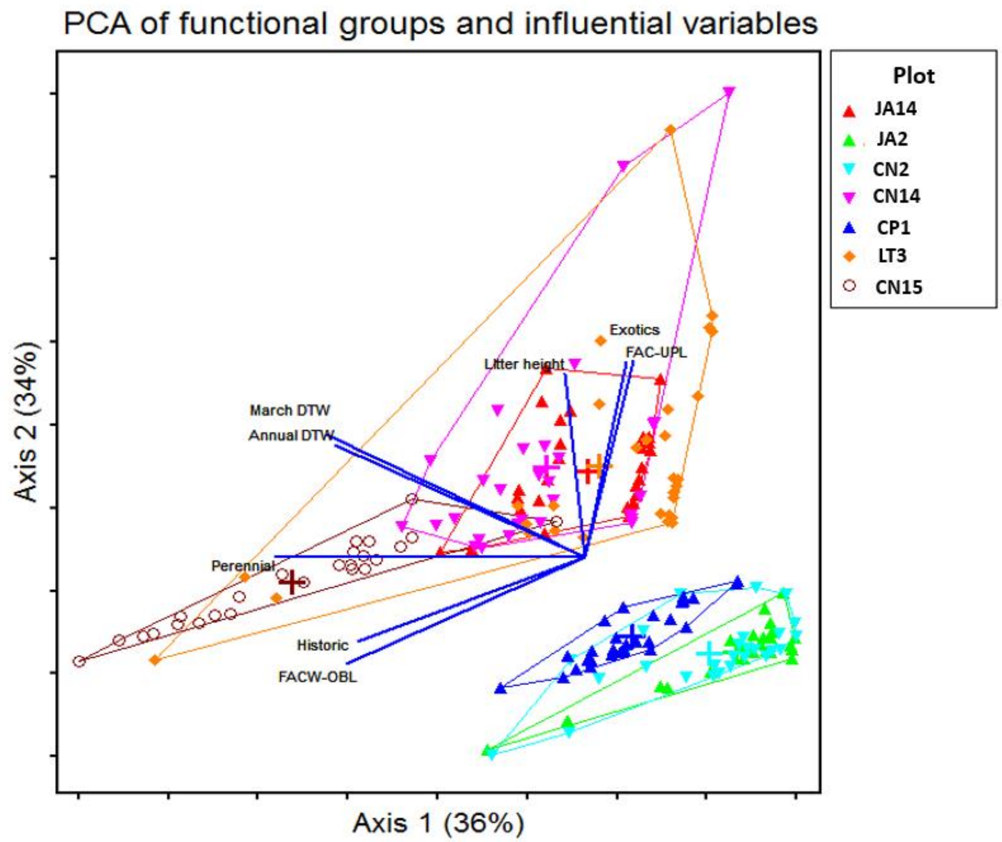
Scientific Name	Common Name	Status/functional group	Wetland Indicator status (FACW/OBL or FAC/UPL)	Historic late seral species used in analysis (yes/no)	Seedling total	% of total
Apera interrupta	silky bentgrass	exotic annual grass	FAC/UPL	no	167	6%
Bromus hordeaceus	field brome	exotic annual grass	FAC/UPL	no	4	0%
Bromus arvensis	soft brome	exotic annual grass	FAC/UPL	no	164	6%
Bromus tectorum	cheatgrass	exotic annual grass	FAC/UPL	no	439	16%
Cardamine oligosperma	western bittercress	native biennial forb	FAC/UPL	no	23	1%
Carex nebrascensis	Nebraska sedge	native perennial graminoid	FACW/OBL	yes	17	1%
Carex praegracilis	field sedge	native perennial graminoid	FACW/OBL	yes	44	2%
Cerastium glomeratum	sticky chickweed	exotic annual forb	FAC/UPL	no	83	3%
Cirsium sp.	thistle	exotic biennial forb	FAC/UPL	no	109	4%
Collinsia parviflora	blue-eyed Mary	native annual forb		no	70	3%
Conyza canadensis	Canada horseweed	exotic annual forb	FAC/UPL	no	1	0%
Deschampsia cespitosa	tufted hairgrass	native perennial graminoid	FACW/OBL	yes	365	13%
Epilobium ciliatum	willow herb	native biennial forb	FACW/OBL	yes	213	8%
Erodium cicutarium	storksbill	exotic annual forb	FAC/UPL	no	30	1%
Eucephalus elegans	elegant aster	native perennial forb	FACW/OBL	no	16	1%
Gnaphalium palustre	meadow cudweed	native perennial forb	FACW/OBL	yes	25	1%
Hordeum brachyantherum	meadow barley	native perennial graminoid	FACW/OBL	yes	37	1%

Juncus arcticus	Arctic rush	native perennial graminoid	FACW/OBL	yes	46	2%
Lactuca serriola	prickly wire lettuce	exotic annual forb	FAC/UPL	no	118	4%
Lepidium sp.	pepperweed	native perennial forb	FAC/UPL	no	27	1%
Lomatium sp.	spring parsley	native perennial forb	FAC/UPL	no	2	0%
Lotus purshianus	birds foot trefoil	native annual forb	FAC/UPL	no	6	0%
Lycopus americanus	water hore hound	native perennial forb	FACW/OBL	no	74	3%
Mimulus guttatus	monkey flower	native perennial forb	FACW/OBL	yes	110	4%
Muhlenbergia richardsonii	muhly grass	native perennial graminoid	FACW/OBL	yes	18	1%
Penstemon rydbergii	Rydberg's penstemon	native perennial forb	FACW/OBL	yes	2	0%
Poa compressa	Canadian bluegrass	native perennial graminoid	FACW/OBL	yes	14	1%
Poa pratensis	Kentuckey bluegrass	native perennial graminoid	FAC/UPL	yes	142	5%
Potentilla glandulosa	sticky cinquefoil	native perennial forb	FACW/OBL	yes	1	0%
Sisymbrium altissimum	tumble mustard	exotic annual forb	FAC/UPL	no	27	1%
Taraxacum officinale	dandylion	native perennial forb	FAC/UPL	no	9	0%
Trifolium pratense	red clover	native perennial forb	FAC/UPL	no	13	0%
Veronica sp.	water speedwell	native perennial forb	FACW/OBL	yes	3	0%
Total number of seedlings					2416	100%

N=native, E=exotic, F=forb, G=graminoid, B=biennial

Wetland Indicator status. UPL=upland, FAC=facultative, FACW=facultative wet, OBL=obligate

Appendix F. Bioassay results % total per species



Appendix G. PCA ordination of associations between functional group seedlings with environmental variables. Monte Carlo tests show axis 1 contributing 36% and axis 2 contributing 34% of the variation explained. Variables associated with each axis: Litter (r=0.76 axis 2), annual DTW (r=-0.73 axis 1), FAC-UPL (r=0.82 axis 2), March DTW (r=-0.-76 axis 1), FACW/OBL (r=-0.69 axis 1), historic ESD species (r=-0.66 axis 1), perennials (r=-0.90 axis 1). Results from the PCA analysis resemble similar relationships between functional groups and environmental variables. Litter height is strongly associated with FAC/UPL and exotic species. DTW (annual and March) are predictably associated with perennial vegetation and historic species.